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Pea Seed-borne Mosaic Virus Causing Pea Mottling in Taiwan

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ABSTRACT

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A virus isolate (PS8) causing mottling or mild mosaic foliar symptoms on pea was collected from a field in Ear-Lin area in 1987. The virus was successfully transmitted to pea cultivar "Hsin-Jan" by manual inoculation and by aphids with non-persistent manner. Cytoplasmic cylindrical (CI) and amorphous (AI) inclusions were observed in infected cells by light microscopy. Flexuous rod-shaped particles with mean length of 734 nm were detected in infected leaf extracts. Among twenty four plant species inoculated only pea and broad bean were systemically infected, and the host reactions were similar to those of described pea seed-borne mosaic virus (PSbMV) isolates from the USA. The virus was successfully purified by differential and Cs_2SO_4 equilibrium centrifugation. The purified capsid and CI proteins consisted of single species of protein monomer with molecular weights of 29 and 74 kilo-daltons, respectively. In reciprocal SDS-immunodiffusion tests, PS8 was found serologically indistinguishable from a PSbMV isolate from the USA (provided by G. I. Mink, Washington State Univ, U.S.A.), related to, but distinct from, blackeye cowpea mosaic virus, passionfruit woodiness virus, and potato virus Y, and unrelated to eleven other potyviruses tested. On the basis of these results, PS8 was recognized as an isolate of PSbMV. This is the first record for the occurrence of PSbMV in Taiwan.

(Key words: pea seed-borne mosaic virus, PSbMV, serology, identification, amorphous inclusion)

INTRODUCTION

Pea (*Pisum sativum* L.) is an important crop grown mainly during winter season in Taiwan (14). Among various types of pea for different uses, fresh pod, sweet snap pod and vegetable green are the three major types grown in this island. For different utilization special cultivars are required and selected. For example, "Taichung No. 11" and "Hsin-Jan" are currently the most popular cultivars for production of fresh

pod and sweet snap pod, respectively. In 1987, mild mosaic or mottling foliar symptoms were found on some plants of cultivar "Hsin-Jan" in a field near Ear-Lin area. The disease was later identified to be caused by pea seed-borne mosaic virus (PSbMV). This paper characterizes the virus isolate, designated as PS8, and determines its serological relationships with other potyviruses.

MATERIALS AND METHODS

Virus isolation and maintenance

Isolate of PS8 was obtained from a diseased plant of pea cultivar "Hsin-Jan" collected from Ear-Lin area in 1987. Virus culture was maintained in the same pea cultivar by manual inoculation. Attempts to obtain pure PS8 isolate by single-lesion isolation procedures were not successful because PS8 induced no local lesions on host plants. Instead, we used a single aphid to transmit PS8 from the original diseased plant to a healthy "Hsin-Jan" pea and the latter served as a source culture for later studies.

Host-range tests

PS8 was transmitted mechanically in the host-range trials. At least five plants of each species or cultivars were inoculated. Recovery tests were conducted by back-inoculation of test plants to "Hsin-Jan" pea. Inoculated plants were kept in a screenhouse for at least one month for observation.

Aphid transmission tests

Aphid transmission trials were conducted with green peach aphids (*Myzus persicae* Sulze.). Aphids were starved 3 hr before access feeding. Individual aphids were given acquisition probes for approximately 60 sec on PS8-infected pea leaves. Groups of 5 aphids were subsequently transferred to each test plant of "Hsin-Jan" Pea. Aphids were removed on the second day and plants placed in screenhouse for observation. The transmission was conducted in duplicate trial each with 20 test plants.

Electron and light microscopy

Virus particles in crude sap of PS8-infected pea leaves were negatively stained in 2 % potassium phosphotungstate (PTA), pH 6.5, containing 0.1% (W/V) bovine serum albumin [5] and observed with a Hitachi 7000 electron microscope. Epidermal strips of healthy and PS8-infected pea leaves were stained either with calcomine orange and "Luxol" brilliant green (O-G) or with Azure A, and examined by light microscopy for virus-induced inclusions [4].

Virus purification and antiserum preparation

PS8 was propagated in Hsin-Jan pea in a screenhouse at about 20-30 C. Infected leaves were harvested 15 days after inoculation and stored overnight in a 4 C cold room before use. The virus was purified by two cycles of differential centrifugations followed by equilibrium centrifugation in Cs_2SO_4 as previously described [3] with some modifications. Triton X-100 was omitted from the previous procedure and 50 mM potassium phosphate buffer, pH 7.5, was substituted for Hepes buffer to resuspend the virus. To obtain antiserum against PS8, four intramuscular injections each with 1 mg of purified virus were administered into rabbits as previously described [3]. Immunized rabbit was bled every week beginning 10 days after the last injection. Antisera obtained were kept in a freezer at –20 C.

Serological tests

Serological relationships of PS8 with other potyviruses were studied by reciprocal SDS-immunodiffusion tests [16]. Antisera and SDS-treated antigens of the following potyviruses were used in this study: peanut

strip [6], potato virus Y [16], tobacco etch [16], watermelon cosaic virus 2 [17], and zucchini yellow mosaic [15] provided by D. E. Purcifull, and bean common mosaic [7], bean yellow mosaic [11], blackeye cowpea mosaic [1], clover yellow vein [8], papaya ringspot virus type W [17], passionfruit mottle [2], passionfruit woodiness [2], soybean mosaic virus (C. -A. Chang, unpublished) were from our own collections. Antiserum, but not antigen, against an isolate of PSbMV provided by G. I. Mink was also included in this study.

Polyacrylamide gel electrophoresis of viral proteins

Cylindrical inclusions were paritally purified by a previously described procedure [3]. Viral proteins were analyzed by discontinuous SDS-polyacrylamide gel electrophoreseis [3].

RESULTS

Host-range and symptomatology

Of total of 31 species and cultivars in 5 plant families inoculated with PS8, only *Vicia faba* L. and cultivars of *Pisum sativum* L. were infected (Table 1). Among 5 different pea cultivars tested, 'Early Perfection' was found immune to PS8, while others were susceptible. The infected pea cultivars developed mottle or sometimes mosaic foliar symptoms (Fig. 1), similar to those observed in the field. Infected plants were somewhat shorter than non-infected ones, however, no reduction in plant vigor was noticed. Broad bean (*Vicia faba* L.) was infected by PS8 without showing any symptoms. This was confirmed by back inoculation to Hsin-Jan pea, by SDS-immunodiffusion tests and by light microscopic detection of PS8-induced inclusions. PS8 induced no detectable local lesions on *C. amaranticolor* Coste & Reyn. and *C. quinoa* Willd..

Aphid transmission trials

A total of forty pea seedlings were tested in two replicate trials with *Myzus persicae* as vectors. Twenty five plants were later found infected. The aphid became infective following an acquisition feeding

Fig. 1. Mottling symptom on 'Hsin-Jan' pea leaf caused by PS8 isolate of pea seed-borne mosaic virus from Taiwan.

Table 1. Host range and reactions of PS8 isolate of pea seed-borne mosaic virus in Taiwan

Test Plant	Reactions [1]	Recovery [2]
Chenopodiaceae		
Chenopodium quinoa	–	–
C. amaranticolor	–	–
Leguminosae		
Pisum sativum cv. 'Hsin-Jan'	M, m	+
P. sativum cv. 'Taichung # 11'	m	+
P. sativum cv. 'Alaska'	m	+
P. sativum cv. 'Dark Skin Perfection'	m	+
P. sativum cv. 'Blackeye'	m	+
P. sativum cv. 'Early Perfection'	–	–
Phaseolus vulgaris cv. 'Top Crop'	–	–
P. vulgaris cv. 'Sutter Pink'	–	–
P. vulgaris cv. 'Dubbele Witte'	–	–
Vigna radiata	–	–
V. mungo	–	–
V. unguiculata subsp. unguiculata	–	–
V. unguiculata subsp. sesquipedalis	–	–
V. angularis	–	–
Glycine max	–	–
Vicia faba	S1	+
Arachis hypogaea cv. 'Tainon No. 4'	–	–
Cassia occidentalis	–	–
Solanaceae		
Nicotiana benthamiana	–	–
N. tabacum cv. 'Havana'	–	–
N. debnyii	–	–
Lycopersicum esculentum	–	–
Datura stramonium	–	–
Amaranthaceae		
Gomphrena globosa	–	–
Cucurtibaceae		
Cucumis sativus	–	–
C. melo	–	–
Citrullus vulgaris	–	–
Momordica charantia	–	–
Luffa cylindrica	–	–

1) M: Mosaic; m: mottle; S1: symptomless; –: no infection.
2) Recovery tests were done one week and one month after inoculation for inoculated and systemic leaves, respectively, by back-inoculation to Hsin-Jan pea.

period of only 60-second, indicating that PS8 is non-persistently transmitted by aphid.

Microscopical studies

Flexuous rod-shaped particles were consistently observed in negatively stained PS8-infected pea leaf extracts. Particles with similar morphology and length were also observed in purified PS8 preparations. Measurement of 117 purified virus particles revealed a mean length of 734 nm. Under light microscopy, cytoplasmic cylindrical inclusions (CI) were consistently observed in epidermal cells of PS8-infected pea and broad bean leaves processed with O-G staining (Fig. 2). The CIs were observed as granular aggregates of short plate-like structures and they were found always sitting closely beside nuclei (Fig. 2). Structures similar to those reported as amorphous inclusions (AI) for pepper mottle virus (PeMV) and papaya ringspot virus type W (PRV-W)[4] were also found in epidermal cells of pea and broad bean leaves (Fig. 2). They were stained green with O-G stains and in pink color with Azure A stains, similar also to those reported for PRV-W and PeMV-induced AIs.

Purification and serology

PS8 was successfully purified by a modified procedure as described for purification of bean yellow mosaic virus[3]. Purified PS8 had a UV absorption spectrum typical of potyviruses with a maximum absorption peak appearing at 260 nm and a minimum absorption one at 247 nm. The ratio for OD 260/280 was 1.23-1.25 in four replicate trials. Assuming an extinction coefficient of 2.4 for PS8 [10], the resulted virus yield was about 2-3 mg per 100 g infected pea tissue. The antiserum produced against PS8 reacted strongly with its homologous antigens but not with healthy pea leaf extract in SDS-immunodiffusion tests (Fig. 3). The highest homologous titer recorded was 1/16 among different bleedings as determined by SDS-immunodiffusion tests using crude sap as antigen. Heterologously, PS8 antiserum reacted weakly, with spur reactions, against antigens of blackeye cowpea mosaic virus and potato virus Y but not with antigens of 11 other potyviruses (Table 2). In reciprocal SDS-immunodiffusion tests, only antisera to blackeye cowpea mosaic virus, passionfruit woodiness virus, potato virus Y and PSbMV cross-reacted with PS8 antigen. Among them, PSbMV antiserum had the strongest reaction to PS8 antigen and the precipitation lin was not spurred over by the homologous PS8 precipitation line (Fig. 3). The other three antisera reacted only weakly and with spurs against PS8 antigen (Table 2). Furthermore, the cross-reactivities of both PSbMV and PS8 antisera to various potyvirus antigens were found identical (Table 2).

Electrophoresis of viral proteins

Monomers of 29 and 74 K corresponding to PS8 purified virus and cylindrical inclusion protein, respectively, were detected in 7.5-15 % gradient polyacrylamide gels (Fig. 4). Besides the major 74 K protein band and trace of 29 K coat protein band, the partially purfied CI sample contained many other minor protein bands. These proteins also occurred in samples purified from healthy pea leaves by same procedures and are considered of host origin.

DISCUSSION

Based on particle morphology and length, aphid transmissibility and the ability to induce CI in infected cells, the PS8 isolate is clearly classified in the potyvirus group [10]. So far, there have been five different potyviruses, i.e. bean yellow mosaic, pea seed-borne mosaic, watermelon mosaic 2, lettuce mosaic, and turnip mosaic viruses, reported to occur naturally in peas [8].

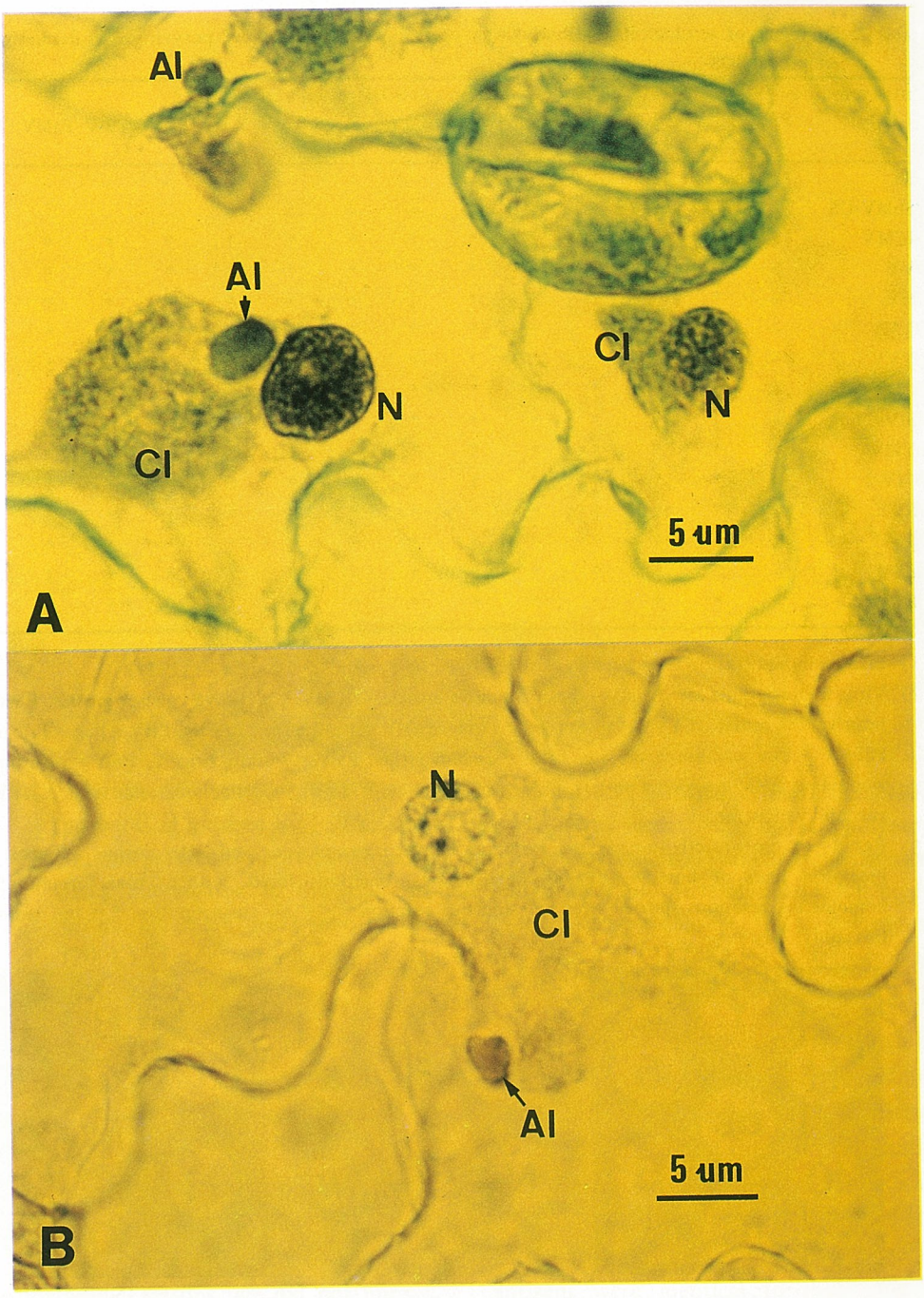

Fig. 2. Light micrographs of epidermal cells of 'Hsin-Jan' pea infected by PS8 isolate of pea seed-borne mosaic virus. A, PS8-induced cylindrical inclusions (CI) and amorphous inclusions (AI) stained with luxol brilliant green/calcomine orange (O-G). B, PS8-induced CI and AI but stained with Azure A. Note that CI is stained green by O-G but is not stained by Azure A, while AI is stained green and pink by O-G and Azure A, respectively.

Table 2. Summary of serological relationships between PS8 and some other potyviruses as determined in reciprocal SDS-immunodiffusion tests[1)]

Antiserum to	Cross-reactivities to SDS-treated antigens of [2)]													
	PS8	PStV	BIC-MV	PVY	BCMV	WMV-2	SMV	BY-MV	CYVV	ZY-MV	PRV	PWV	PaMV	TEV
PS8	I [3)]	–	S	S	–	–	–	–	–	–	–	–	–	–
PSbMV-US	I	–	S	S	–	–	–	–	–	–	–	–	–	–
BICMV	S	*	I	*	*	*	*	*	*	*	*	*	*	*
PVY	S	*	*	I	*	*	*	*	*	*	*	*	*	*
SMV	–	*	*	*	*	*	I	*	*	*	*	*	*	*
BYMV	–	*	*	*	*	*	*	I	*	*	*	*	*	*
CYVV	–	*	*	*	*	*	*	*	I	*	*	*	*	*
BCMV	–	*	*	*	I	*	*	*	*	*	*	*	*	*
PStV	–	I	*	*	*	*	*	*	*	*	*	*	*	*
ZYMV	–	*	*	*	*	*	*	*	*	I	*	*	*	*
WMV-2	–	*	*	*	*	I	*	*	*	*	*	*	*	*
PRV	–	*	*	*	*	*	*	*	*	*	I	*	*	*
PWV	S	*	*	*	*	*	*	*	*	*	*	I	*	*
PaMV	–	*	*	*	*	*	*	*	*	*	*	*	I	*
TEV	–	*	*	*	*	*	*	*	*	*	*	*	*	I

1) SDS-immunodiffusion tests were done as described by Purcifull and Batchelor (1977).

2) Virus abbreciations are: BCMV = bean common mosaic, B1CMV = blackeye cowpea mosaic, BYMV = bean yellow mosaic, CYVV = clover yellow vein, PaMV = passionfruit mottle, PRV = papaya ringspot, PSbMV = pea seed-borne mosaic, PStV = peanut stripe, PVY = potato virus Y, PWV = possionfruit woodiness, SMV = soybean mosaic, TEV = tobacco etch, WMV-2 = watermelon mosaic virus 2, ZYMV = zucchini yellow mosaic.

3) Results of cross-reactivities are the reactions between homologous and heterologous antigens: I = Precipitin lines of homologous and heterologous reactions fused, without spur formation; S = homologous reactions spurred over heterologous reactions; – = no cross-reaction; * = not tested in this study.

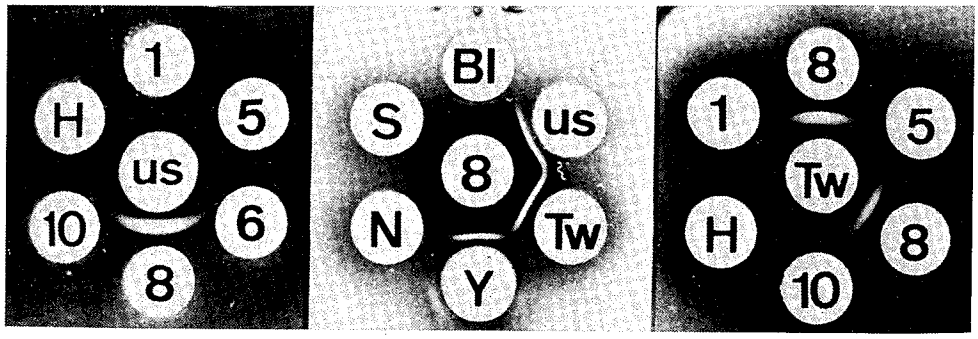

Fig. 3. Sodium dodecyl sulfate (SDS)-immunodiffusion tests with the PS8 isolate of pea seed-borne mosaic virus (PSbMV) and some other virus isolates collected from field grown pea. The SDS-treated extracts of virus-infected tissue were used as antigens to react with undiluted antisera as described in the text. Antisera used in this study were against: PSbMV from the U.S.A. provided by G. I. Mink (US), PS8 isolate of PSbMV from Taiwan (Tw), blackeye cowpea mosaic virus (B1), potato virus Y (Y) and soybean mosaic virus (S). Preimmune normal serum (N) was included as control. The SDS-treated antigens used were: PS8 isolate of PSbMV (8), three isolates of peanut mottle virus (1, 5, and 10), and one unknown virus isolate (6) all collected from field grown pea plants in Taiwan and healthy pea control (H).

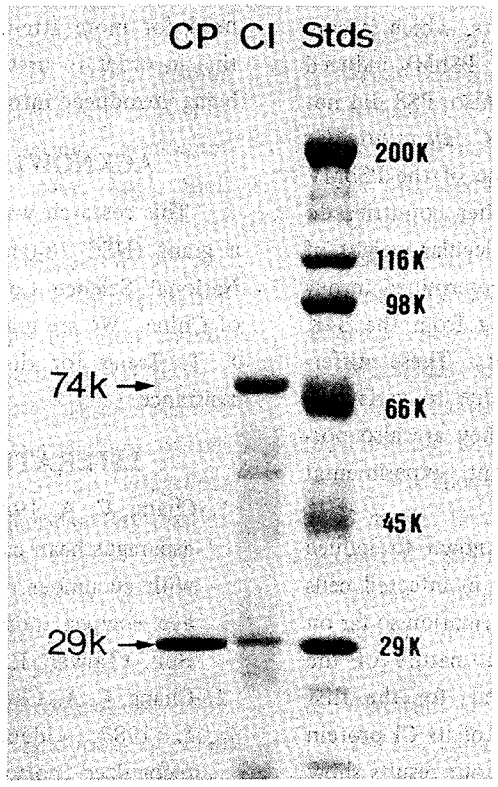

Fig. 4. Analysis of purified capsid protein (CP) and partially purified cylindrical inclusion protein(CI) induced by PS8 isolate of pea seed-borne mosaic virus by SDS-polyacrylamide gel electrophoresis. Molecular weight (MW) standards (Stds) in kilo-daltons are from the bottom to the top: carbonic anhydrase (29K), ovalbumin (45K), bovine serum albumin (66K), phosphorylase B (98K), galactosidase (116K), and myosin (200K). Estimated MW of PS8-induced CP (29K) and CI (74K) are indicated on the left side of the figure.

Among them, PSbMV, but not the other four, has many properties similar to what we found on PS8[8,9,12]. Both viruses have a limited host range, and restrict their systemic infectivities only in peas and broad beans [9]. In addition, they are nearly identical in serological properties. Although, for quarantine reasons, we did not import PSbMV isolates from other country to serve as referece antigens in serological comparisons with PS8, we tend to believe that PS8 is serologically indistinguishable from PSbMV. This is based on the following observations: 1). Fourteen different potyvirus antisera used in this study, only PSbMV antiserum provided by G. I. Mink (Washington State Univ., U.S.A.) reacted, as strongly as the homologous PS8 antiserum, with PS8 antigen and the two precipitation lines fused together without any spurs (Fig. 3). 2). The cross-reactivities of PSbMV antiserum against 13 different potyvirus antigens were identical to those of PS8 antiserum against the same set of antigens (Table 2). Consequently, PS8 should be recognized as an isolate of PSbMV. Nevertheless, there are some minor differences between PS8 and other PSbMV isolates reported so far. First of all, on all five pea cultivars tested, PS8 did not induce down-

ward rolling of pea leaflets, which is considered a characteristic PSbMV-induced symptom on pea [9,12]. Also, PS8 did not induce local lesions on *C. amaranticolor* and *C. quinoa,* while some of the PSbMV isolates reported from other countries do [9]. In addition, the molecular weight of capsid protein of PS8 is determined in our test to be 29 K, differing from the 34K reported for PSbMV [9]. These differences, however, may be due to variations between virus isolates. They are also possibly caused by different experimental conditions.

Although PSbMV is known to induce CIs or pinwheel inclusions in infected cells [9], there has been no information so far on the chemical and physical nature of the inclusions. We determined, for the first time, the molecular weight of its CI protein to be 74 K. Furthermore, our results show that PS8 induces not only CI but also inclusions similar to AI in infected cells. Whether it is a common feature for all PSbMV isolates to induce AI-like inclusions should deserve further studies. If confirmed, the AI-like inclusions can be used as a valuable cytological marker for distinguishing PSbMV from other pea-infecting legume viruses.

In conclusion, the PS8 isolate obtained from Hsin-Jan pea is identified as an isolate of PSbMV. This provides the first evidence of the occurrence of PSbMV in Taiwan. Since PSbMV is known for its high seed-transmission rate [9,12], it is highly possible that the virus is introduced into Taiwan through imported contaminated seed lots. Considering the difficulty in controlling seed-transmissible viruses, especially when the virus can be further disseminated from infected seedlings to healthy plants by aphids as shown for PS8, we emphasize a need for more attentions on plant quarantine in order to prevent other viruses from being introduced into this island.

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引起豌豆葉部斑紋病徵之豌豆種媒嵌紋病毒之鑑定

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（接受日期：民國78年10月30日）

摘　要

張清安、陳建名、陳慧琦、鄧汀欽、黃秋雄 1989 引起豌豆葉部斑紋病徵之豌豆種媒嵌紋病毒之鑑定 植保會刊31：366-376

民國76年由二林地區所栽植之新珍甜豌豆分離獲得一個病毒分離株（PS8），可於新珍豌豆葉部造成輕微斑紋至嵌紋病徵。在實驗室中PS8可經由人工接種及桃蚜媒介至健全豌豆，並造成相同病徵，於光學顯微鏡下罹病株葉片下表皮細胞內可觀察到PS8所形成之圓柱狀內含體（CI）及不定形內含體（AI）。於電子顯微鏡下可於罹病植株汁液中發現平均長度約734nm之長絲狀病毒顆粒。接種5科24種植物發現，PS8只能感染豌豆及蠶豆。此種窄狹之寄主範圍特性與國外報告之豌豆種媒嵌紋病毒極其類似。經高低速交替及密度階層平衡離心，吾人已將PS8由豌豆中純化成功，其鞘蛋白及圓柱狀內含體蛋白之分子量分別經電泳分析估計為29K及74K。在血清學鑑定方面，供試之14種抗血清中，唯有由美國華盛頓州立大學G.I.Mink所提供之PSbMV抗血清可與PS8抗原反應，而且其反應沈澱帶與PS8同源沈澱帶癒合，顯示二者間血清性質極為接近。再加上PSbMV抗血清與供試13種不同 PVY群病毒抗原之反應關係與PS8抗血清所獲結果完全相同，因此進一步證實PSbMV與PS8間血清性質應完全相同，PS8與黑眼豇豆嵌紋病毒（BlCMV），馬鈴薯Y病毒（PVY）及百香果木質化病毒（PWV）具血清類緣關係，但與其他11種供試病毒不具血緣關係。由各項特性鑑定PS8應屬豌豆種媒嵌紋病毒之一分離株。此乃 PSbMV發生於本省之首次記錄。

（關鍵字：豌豆種媒嵌紋病毒，血清學，鑑定）